Quantitative Assessment of Biotic Mortality Factors of the European Corn Borer (Lepidoptera: Crambidae) in Field Corn

MPHO W. PHOOFOLO,[1] JOHN J. OBRYCKI, AND LESLIE C. LEWIS[2]

Department of Entomology, Iowa State University, Ames, IA 50011–3140

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ABSTRACT Five treatments were used to exclude naturally occurring predators and parasitoids, based on body size and flight ability, to assess their effect on *Ostrinia nubilalis* (Hübner) populations on corn plants. Two initial *O. nubilalis* egg densities (one egg mass and three egg masses per plant) were assigned to each treatment. Egg predation was higher in uncaged treatments than in caged treatments. Flying insect predators, primarily *Coleomegilla maculata* DeGeer (Coleoptera: Coccinellidae), reduced egg densities by 50%. Thirty-five to 84% of *O. nubilalis* larvae were infected with *Nosema pyrausta* (Paillot) (Microspora: Nosematidae). The incidence of *Beauveria bassiana* (Balsamo) Vuillemin (Deuteromycotina: Hyphomycetes), ranged from 0 to 21%, whereas larval parasitism, mainly by *Macrocentrus cingulum* Reinhard (Hymenoptera: Braconidae) ranged from 0 to 31%. In contrast to previous studies, this 3-yr field study documents that egg predation and larval infections of *O. nubilalis* were significant and consistent biotic mortality factors.

KEY WORDS *Coleomegilla maculata, Nosema pyrausta, Ostrinia nubilalis,* biological control, natural control, predation

THE EUROPEAN CORN borer, *Ostrinia nubilalis* (Hübner), is attacked by natural enemies throughout its range in North America. Several species of natural enemies were introduced, either intentionally or accidentally, whereas others are indigenous predators that adapted to it as prey (Baker et al. 1949, Clausen 1978, Hudon et al. 1989). The introduced species *Macrocentrus cingulum* Reinhard, previously *Macrocentrus grandii* Goidanich (Hymenoptera: Braconidae) (van Achterberg and Haeselbarth 1983) and *Eriborus terebrans* (Gravenhorst) (Hymenoptera: Ichneumonidae) are relatively common parasitoids of *O. nubilalis* in the Midwest (Lewis 1982, Siegel et al. 1987a, Landis and Haas 1992, Clark et al. 1997). Two entomopathogens that infect *O. nubilalis* are the microsporidium, *Nosema pyrausta* (Paillot) (Microspora: Nosematidae) (Zimmack and Brindley 1957, Lewis and Cossentine 1986, Siegel et al. 1987b), and the fungus, *Beauveria bassiana* (Balsamo) Vuillemin (Deuteromycotina: Hyphomycetes) (Bing and Lewis 1993). Several indigenous predatory species attack *O. nubilalis* eggs and early instars, including the coccinellid *Coleomegilla maculata* DeGeer (Coleoptera: Coccinellidae), two Chrysopidae species [*Chrysoperla carnea* (Stephens) and *Chrysopa oculata* Say] (Neuroptera: Chrysopidae), and *Orius* species (Heteroptera: Anthocoridae) (Obrycki et al. 1989, Andow 1990, Coll and Bottrell 1992, Phoofolo and Obrycki 1997, Phoofolo et al. 1999).

Several other factors cause mortality of *O. nubilalis*, e.g., drowning in plant sap or rain that accumulates in the plant whorl, cultural practices, larval movement, and adult migration (Chiang and Hodson 1972, Showers et al. 1978, Hudon and LeRoux 1986, Ross and Ostlie 1990). Previous studies have identified insect predators as important sources of *O. nubilalis* egg mortality (Sparks et al. 1966, Frye 1972). However, Sparks et al. (1966) concluded that although the impact of insect predators was high, it was not spatially or temporally consistent. Despite these mortality factors, larval densities of *O. nubilalis* occasionally reach levels that reduce yields (Mason et al. 1996). To develop an integrated control program for *O. nubilalis*, we designed this study to assess levels of naturally occurring mortality of *O. nubilalis* eggs and larvae and to quantify mortality caused by predators, parasitoids, and pathogens.

Materials and Methods

The experiment was conducted in field corn, *Zea mays* L., in Story County, IA, from 1994 to 1996. The same corn hybrid (Pioneer 3563) and cultivation practices (conventional tillage, fertilizer and herbicide application, but no insecticides) were used each year. Tassel stage corn (R1) was used in 1994, whorl stage corn (V6–8) in 1996, and both stages were used in 1995 (Ritchie et al. 1997). Five treatments were used to evaluate natural enemies of *O. nubilalis:* (1) open areas (of equal size to those covered by cages) that

[1] Current address: Department of Biology, National University of Lesotho, Lesotho.

[2] USDA-ARS, Corn Insects and Crop Genetics Research Unit, Iowa State University.

allowed all natural enemies access to *O. nubilalis;* (2) open areas as in (1) but each corn plant had a thick ring of tack trap (Tanglefoot, Grand Rapids, MI) applied 5 cm above the ground to exclude ground-dwelling nonflying predators (e.g., Formicidae, Carabidae, and Araneae); (3) open frames (1.6 by 1.6 by 1.6 m) that were covered with small-size mesh cages (52 squares/cm^2) from the top of the metal frames to within 1 m of the ground to shade plants, i.e., this treatment simulated the cage effects of treatment (5); (4) large-size mesh (32 squares/cm^2) Lumite (Chicopee Manu, Gainesville, GA) cages (1.6 by 1.6 by 1.6 m) that allowed access by small predators (e.g., *Orius insidiosus,* early instars of Coccinellidae and Chrysopidae, and Formicidae) and parasitoids; and (5) small-size mesh (52 squares/cm^2) Lumite cages (1.6 by 1.6 by 1.6 m) that excluded all predators and parasitoids. There were 16 plants (8 per row) for each treatment.

Each of the five treatments had two infestation levels of *O. nubilalis* egg masses, one or three per plant, and two replications, i.e., a total of 20 plots. Compared with natural infestations of *O. nubilalis,* one egg mass per plant would be equivalent to a heavy infestation; three egg masses per plant would not likely occur in nature, but was included to allow adequate assessment of natural enemies. The treatments were blocked and randomly assigned to plots. Egg masses, (≈30 eggs per mass), attached to waxed paper disks, were produced by the USDA-ARS Corn Insects and Crop Genetics Research Unit (Guthrie et al. 1985). This *O. nubilalis* colony was reared in the laboratory for <1 yr and was not infected with *N. pyrausta* or *B. bassiana.* The timing of this study was synchronized with the occurrence of the two *O. nubilalis* generations in Iowa (June and August). Egg masses (<24 h old) simulating the first generation were randomly stapled on the undersides of leaves in mid- to late whorl stage corn (55–80 cm extended leaf height). For the second generation, egg masses (<24 h old) were stapled on the undersides of the middle seven leaves (the ear leaf and the three leaves above and below the ear) of tassel stage corn. The egg masses were attached between the midrib and edge of the leaves. The egg masses were placed on the plants over 8 d; two plants per treatment were randomly selected to be infested each day.

Each cohort of eggs was monitored twice per week, using a 20×-field magnifying glass, to determine the fate of eggs. Egg predation from chewing predators was distinguished from predation from piercing-sucking predators as outlined by Andow (1990). Egg predation was expressed as a percentage of total egg masses attacked. The criterion used for categorizing egg masses as preyed upon was when ≥50% of the eggs within an egg mass were preyed upon. The reason for this criterion is that eggs within an egg mass that escape predation usually do not hatch because of dessication or infection by saprophytic fungi (Lynch and Lewis 1978).

Ostrinia nubilalis larvae were collected twice a week through destructive sampling of two plants from each plot. A plastic bag (2 by 1 by 1 m) was placed over the plant to be sampled and pulled down to the ground level, then the plant was cut at the base. Bagged plants were brought to the laboratory where each plant and the bag were examined for *O. nubilalis* larvae.

On each sampling date, live larvae were collected and reared individually on meridic diet in 20-ml plastic cups (Lewis and Lynch 1969). Dead larvae found on plants or inside the plastic bags were frozen and examined for infection by *N. pyrausta* and *B. bassiana.* Infections by *N. pyrausta* were determined by preparing wet mounts of the homogenized abdomen of a specimen and looking for spores using a phase contrast microscope at 400×. Infections by *B. bassiana* were determined by placing the thorax of a specimen on a selective medium that favored the growth of *B. bassiana* (Doberski and Tribe 1980). Parasitism was determined by rearing *O. nubilalis* larvae; all parasitized hosts and parasitoids were examined for *N. pyrausta.* Pupae were reared to adult eclosion or death and examined for disease development. Individuals that survived to the adult stage were examined for *N. pyrausta* by homogenizing their abdomen and preparing wet mounts.

Egg predation levels, disease prevalence, and parasitism levels were analyzed using a two-way analysis of variance (ANOVA) of the general linear models (PROC GLM) in SAS (two factors were cage treatments and blocks) (SAS Institute 1985). Data from different years and plant stages were analyzed separately. Data in percentages were first normalized using

Table 1. Mean ± SE percentage of *Ostrinia nubilalis* egg masses that hatched and percentage of egg masses that were preyed upon or died from unknown causes at two infestation levels on tassel stage corn in 1994

Treatment	1 egg mass per plant			3 egg masses per plant		
	Hatched	Preyed upon	Unknown	Hatched	Preyed upon	Unknown
No Cage	25.0 ± 7.7a	62.5 ± 8.6a	12.5	41.0 ± 5.2a	50.1 ± 4.9a	8.9
Tack Trap	21.9 ± 7.3a	62.5 ± 8.6a	15.6	32.7 ± 4.0a	57.6 ± 3.9a	9.7
Shaded	26.6 ± 7.7a	64.1 ± 8.4a	9.3	35.0 ± 3.9a	56.7 ± 3.9a	9.7
Large-mesh Cage	54.7 ± 8.8b	32.8 ± 8.2b	12.5	65.3 ± 3.4b	24.2 ± 3.7b	10.5
Small-mesh Cage	71.6 ± 7.5b	22.2 ± 7.0b	6.2	69.3 ± 4.9b	20.6 ± 2.9b	10.1
F	7.7	5.7		14.6	23.5	
df	4,150	4,150		4,149	4,149	
P	<0.01	<0.01		<0.01	<0.01	

Means within a column followed by the same letter are not significantly different.

Table 2. Mean ± SE percentage of *Ostrinia nubilalis* egg masses that hatched and percentage of egg masses that were preyed upon or died from unknown causes at two infestation levels on whorl stage corn in 1995

Treatment	1 egg mass per plant			3 egg masses per plant		
	Hatched	Preyed upon	Unknown	Hatched	Preyed upon	Unknown
No Cage	37.5 ± 3.7a	53.1 ± 5.6a	9.4	38.7 ± 4.0a	43.8 ± 5.3a	17.5
Tack Trap	49.7 ± 2.9a	40.9 ± 3.8a	9.4	50.7 ± 4.9ab	40.1 ± 4.4a	9.2
Shaded	73.4 ± 8.4b	20.3 ± 2.7b	6.3	61.0 ± 5.8b	31.8 ± 5.3a	7.2
Large-mesh Cage	76.6 ± 6.2b	12.5 ± 2.6b	10.9	75.0 ± 4.5c	18.8 ± 3.7b	6.2
Small-mesh Cage	92.2 ± 8.9b	4.7 ± 3.2b	3.1	88.7 ± 2.8d	7.3 ± 2.4b	4.0
F	9.0	8.8		19.3	12.2	
df	4,150	4,150		4,150	4,150	
P	<0.01	<0.01		<0.01	<0.01	

Means within a column followed by the same letter are not significantly different.

arcsine transformation. Untransformed means and standard errors are presented. When significant differences were observed, the least significant difference (LSD) test was used for pair-wise comparisons among treatments (SAS Institute 1985). The significance level for all tests was $P = 0.05$.

Voucher specimens are in the Iowa State University Insect Collection, Department of Entomology, Ames, IA.

Results

Fate of *Ostrinia nubilalis* Eggs. The percentage of *O. nubilalis* eggs that hatched was always higher among egg masses on caged plants than among egg masses on uncaged plants (Tables 1–4). The only exception was on the 1995 whorl stage corn infested with one egg mass per plant; in which egg masses on plants that were in the shaded treatment hatched at levels that were similar to those on caged plants (Table 2).

Predation levels were significantly higher among egg masses on uncaged plants than among egg masses on caged plants (Tables 1–4). With the exception of the 1996 whorl stage corn, predation levels of eggs in large-meshed cages were not significantly different from those of eggs in small-meshed cages. This indicates that despite the mesh size large enough to allow small predators through, the cages presented a barrier to these predators. Predation levels in shaded plants were significantly different from those in caged plants (Tables 1–4). The only exception was on the 1995 whorl stage corn infested with one egg mass per plant (Table 2). This indicates that shading did not negatively affect predators.

Throughout the study, chewing predators accounted for >70% of the total predation (75% in 1994 tassel stage corn, 77% in 1995 whorl stage corn, 73% in 1995 tassel stage corn, and 83% in 1996 whorl stage corn). The remaining predation was due to piercing-sucking predators.

Another trend observed throughout the study was the similarity in hatching and predation levels between the two infestation levels across and within treatments. The *t*-test on hatching levels for the 1994 tassel stage corn gave *t*-values that ranged from 0.25 to 1.72 (df = 62) for all treatments, and *P* values ranged from 0.09 to 0.80. For predation levels, *t*-values ranged from 0.09 to 0.68 (df = 62) for all treatments, and *P* values ranged from 0.50 to 0.93. The *t*-test on hatching levels for the 1995 whorl stage corn gave *t*-values that ranged from 0.08 to 1.28 (df = 62) for all treatments, and *P* values ranged from 0.20 to 0.93; for predation the *t*-values ranged from 0.09 to 1.29 (df = 62) for all treatments, and *P* values ranged from 0.20 to 0.93. The *t*-test on hatching levels for the 1995 tassel stage corn gave *t*-values ranging from 0.06 to 0.99 (df = 62) for all treatments, and *P* values ranged from 0.33 to 0.95. For predation levels, *t*-values ranged from 0.22 to 1.40 (df = 62) for all treatments, and *P* values ranged from 0.17 to 0.82. The *t*-values for hatching levels from the 1996 whorl stage corn ranged from 1.14 to 1.95 (df = 62) for all treatments, and *P* values ranged from 0.19 to 0.87; and for predation levels, *t*-values ranged from

Table 3. Mean ± SE percentage of *Ostrinia nubilalis* egg masses that hatched and percentage of egg masses that were preyed upon or died from unknown causes at two infestation levels on tassel stage corn in 1995

Treatment	1 egg mass per plant			3 egg masses per plant		
	Hatched	Preyed upon	Unknown	Hatched	Preyed upon	Unknown
No Cage	29.7 ± 3.3a	54.7 ± 2.4a	15.6	26.0 ± 3.5a	60.3 ± 6.6a	13.7
Tack Trap	25.0 ± 4.2a	71.9 ± 7.5ab	3.1	24.3 ± 2.6a	68.3 ± 5.9a	7.4
Shaded	10.9 ± 2.3a	79.7 ± 8.3b	9.4	16.0 ± 2.3a	70.3 ± 7.6a	13.7
Large-mesh Cage	79.7 ± 6.8b	17.2 ± 3.2c	3.1	73.3 ± 6.9b	15.7 ± 3.3b	11.0
Small-mesh Cage	76.6 ± 7.4b	23.4 ± 4.1c	0.0	76.0 ± 8.6b	12.6 ± 2.6b	11.4
F	21.4	15.3		30.0	29.8	
df	4,150	4,150		4,150	4,150	
P	<0.01	<0.01		<0.01	<0.01	

Means within a column followed by the same letter are not significantly different.

Table 4. Mean ± SE percentage of *Ostrinia nubilalis* egg masses that hatched and percentage of egg masses that were preyed upon or died from unknown causes at two infestation levels on whorl stage corn in 1996

Treatment	1 egg mass per plant			3 egg masses per plant		
	Hatched	Preyed upon	Unknown	Hatched	Preyed upon	Unknown
No Cage	17.2 ± 3.4a	51.6 ± 4.8a	31.2	29.3 ± 3.3a	59.3 ± 5.6a	11.4
Tack Trap	29.7 ± 4.2ab	57.8 ± 6.4a	12.5	25.0 ± 2.6a	58.3 ± 6.3a	16.7
Shaded	40.6 ± 5.1b	59.4 ± 6.7a	0.0	46.3 ± 4.5b	45.3 ± 4.8b	8.4
Large-mesh Cage	51.6 ± 6.4bc	35.9 ± 4.2b	12.5	54.7 ± 5.7b	28.7 ± 3.3c	16.6
Small-mesh Cage	65.6 ± 6.6c	18.8 ± 2.3c	15.6	74.3 ± 8.6c	9.9 ± 2.6d	15.8
F	6.2	4.6		11.1	15.4	
df	4,150	4,150		4,150	4,150	
P	<0.01	<0.01		<0.01	<0.01	

Means within a column followed by the same letter are not significantly different.

0.29 to 1.16 (df = 62) for all treatments, and *P* values ranged from 0.41 to 0.77.

Prevalence of Disease and Parasitism in *Ostrinia nubilalis* Larvae. Because there were no statistical differences in proportions of diseased and parasitized *O. nubilalis* larvae between plants infested with one or three *O. nubilalis* egg masses, the data from both infestation levels were pooled and analyzed together.

The treatments did not affect infection of *O. nubilalis* larvae by *B. bassiana* throughout the entire study, and the infection levels were always low (i.e., <25%) (Table 5). The infection levels of *O. nubilalis* larvae by *N. pyrausta* were not influenced by treatments, except during the 1995 whorl stage corn (Table 6), when infection levels were significantly lower on the plants in the tack trap treatment (Table 6). Infection levels by *N. pyrausta* were relatively high in all of the studies, varying from 35 to 84% (Table 6). Parasitization rates were not affected by the treatments, except during the 1994 tassel stage corn (Table 7). During that time, parasitization rates on uncaged plants were higher than on caged plants (Table 7). This was the only time when significant rates of parasitization occurred (up to 31% as opposed to a maximum of 8% in the other three tests) (Table 7). *Macrocentrus cingulum* accounted for >95% of the parasitism; *Eriborus terebrans* was rarely found.

Discussion

Previous studies concluded that the effect of insect predators on *O. nubilalis* egg mortality was spatially and temporally inconsistent (Sparks et al. 1966). However, the evaluation by Sparks et al. (1966) has several limitations, which potentially led to misinterpretation of the data. First, *O. nubilalis* eggs in the Sparks et al. (1966) study were at an advanced stage of embryonic development (i.e., black-head stage, ≈4 d old), whereas we used eggs that were <24 h old. Therefore, eggs in the Sparks et al. (1966) study were exposed to predation for a much shorter period than in our study. Second, Sparks et al. (1966) placed *O. nubilalis* egg masses inside the plant whorl, where they may have been concealed and inaccessible to predators. During the whorl stage, *O. nubilalis* females usually deposit egg masses on the undersides of fully emerged leaves (Mason et al. 1996). Finally, the impact of predation in Sparks et al. (1966) was based on comparisons of densities of mature larvae between caged and uncaged plants. Other abiotic and biotic factors, which may have greater influence on larval densities compared with insect predators, can confound the interpretation of the role of predation (Hudon and LeRoux 1986, Mason et al. 1996).

In this study, the effect of insect predators on *O. nubilalis* was evaluated on egg densities, the stage most vulnerable to insect predation (Dicke and Jarvis 1962, Obrycki et al. 1989, Andow 1990). Insect predation accounted for >50% reduction in egg densities. Insect predators frequently observed in our experimental plots were *C. maculata,* two Chrysopidae species (*Chrysoperla carnea* and *Chrysopa oculata*), and *Orius* species. Chewing predators, particularly *C. maculata,* caused most egg predation. This lady beetle species feeds on and completes development on *O. nubilalis* eggs (Phoofolo and Obrycki 1997). Egg predation by piercing-sucking predators was mostly due to chrysopid larvae; a very low proportion of *O. nubilalis* eggs were preyed on by *Orius* species as indicated by the characteristic melanization of egg remains from its feeding (Andow 1990). The effect of ground-dwelling predators on *O. nubilalis* eggs was not significant in our study because predation levels in tack trap and no-cage treatments were similar.

Among larvae collected from the five treatments, high levels of infection by *N. pyrausta* were observed, compared with percentages of larvae either infected by *B. bassiana* or parasitized by *M. cingulum.* However, unlike *B. bassiana* and parasitoids, which directly kill their hosts, *N. pyrausta* infections are chronic. Indi-

Table 5. Mean (SE) percentage of *Ostrinia nubilalis* larvae that were infected with *Beauveria bassiana*, 1994–1996

Treatment	1994TS	1995WS	1995TS	1996WS
No cage	16.2 (1.4)	7.7 (0.5)	7.9 (0.3)	0.0 (0.0)
Tack trap	13.6 (0.9)	11.4 (2.0)	9.1 (1.1)	2.3 (0.6)
Shaded	21.4 (1.7)	10.7 (0.6)	10.5 (0.8)	0.0 (0.0)
Large meshed	11.9 (0.6)	2.1 (0.3)	5.5 (0.4)	6.1 (1.2)
Small meshed	11.4 (0.4)	5.9 (1.4)	8.7 (0.7)	5.7 (1.6)
F	0.44	1.75	1.56	1.22
df	4,123	4,222	4,210	4,108
P	0.78	0.14	0.91	0.31

WS, whorl stage corn; TS, tassel stage corn.

Table 6. Mean (SE) percentage of *Ostrinia nubilalis* larvae that were infected with *Nosema pyrausta*, 1994–1996

Treatment	1994TS	1995WS	1995TS	1996WS
No cage	83.1 (7.5)	51.3 (6.5) a	59.1 (4.4)	43.0 (5.1)
Tack trap	77.8 (8.4)	35.1 (4.6) b	51.3 (4.8)	39.9 (6.2)
Shaded	84.6 (4.6)	64.7 (5.3) a	66.0 (4.2)	47.9 (4.7)
Large meshed	84.2 (4.2)	65.4 (4.8) a	63.7 (3.4)	43.7 (6.4)
Small meshed	80.4 (3.8)	71.5 (7.2) a	64.4 (5.2)	62.9 (2.5)
F	0.46	6.53	1.24	0.82
df	4,118	4,221	4,210	4,107
P	0.76	<0.01	0.98	0.51

WS, whorl stage corn; TS, tassel stage corn. Means within a column for a corn stage followed by a different letter are significantly different.

viduals infected by *N. pyrausta* have reduced adult longevity and fecundity, as well as increased larval mortality (Kramer 1959, Lewis and Lynch 1976, Windels et al. 1976). But, because of its high prevalence, multiple modes of transmission, effects on reproductive capacity, and interactive ability with other mortality factors, *N. pyrausta* is probably a key factor in the population dynamics of *O. nubilalis* (Lewis and Lynch 1976, Siegel et al. 1986).

The incidence of *B. bassiana* was highest in 1994; 21.4% of collected *O. nubilalis* larvae were infected. The overall infection levels we observed were lower than levels observed (84%) by Bing and Lewis (1993) among overwintering larvae. Thus, the effect of *B. bassiana* appears to be greatest on the overwintering population of *O. nubilalis* larvae (L.C.L., unpublished data). With the exception of 1994 when parasitism levels peaked at 31.1%, the impact of *M. cingulum* on reducing *O. nubilalis* densities was relatively small. Similarly, low levels of parasitism by *M. cingulum* have been observed in Illinois and Nebraska (Siegel et al. 1987a, Clark et al. 1997).

Previous studies have reported high levels of preimaginal *O. nubilalis* mortality (Showers et al. 1978, Hudon and LeRoux 1986, Siegel et al. 1987a, Coll and Bottrell 1992). It appears that *O. nubilalis* is similar to other stalk boring insects, which persist as pests despite suffering high generational mortalities, largely due to their high reproductive potential (Tucker 1934, Hudon and LeRoux 1986).

Table 7. Mean (SE) percentage of *Ostrinia nubilalis* larvae that were parasitized, 1994–1996

Treatment	1994TS	1995WS	1995TS	1996WS
No cage	31.1 (5.1) a	1.5 (1.6)	1.2 (2.6)	0.0 (0.0)
Tack trap	29.4 (4.8) a	0.0 (0.0)	0.6 (1.8)	7.9 (8.2)
Shaded	30.0 (4.6) a	5.0 (5.2)	6.3 (6.4)	0.0 (0.0)
Large meshed	7.9 (2.3) b	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Small meshed	0.0 (0.0) c	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
F	8.93	2.13	1.34	0.47
df	4,70	4,204	4,198	4,83
P	<0.01	0.08	0.09	0.76

WS, whorl stage corn; TS, tassel stage corn. Means within a column for a corn stage followed by a different letter are significantly different.

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